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Decline in atmospheric sulphur deposition and changes in climate are the major drivers of long-term change in grassland plant communities in Scotland☆

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ABSTRACT

The predicted long lag time between a decrease in atmospheric deposition and a measured response in vegetation has generally excluded the investigation of vegetation recovery from the impacts of atmospheric deposition. However, policy-makers require such evidence to assess whether policy decisions to reduce emissions will have a positive impact on habitats. Here we have shown that 40 years after the peak of SO_x emissions, decreases in SO_x are related to significant changes in species richness and cover in Scottish Calcareous, Mestrophic, *Nardus* and Wet grasslands. Using a survey of vegetation plots across Scotland, first carried out between 1958 and 1987 and resurveyed between 2012 and 2014, we test whether temporal changes in species richness and cover of bryophytes, Cyperaceae, forbs, Poaceae, and Juncaceae can be explained by changes in sulphur and nitrogen deposition, climate and/or grazing intensity, and whether these patterns differ between six grassland habitats: Acid, Calcareous, *Lolium*, *Nardus*, Mesotrophic and Wet grasslands. The results indicate that Calcareous, Mesotrophic, *Nardus* and Wet grasslands in Scotland are starting to recover from the UK peak of SO_x deposition in the 1970's. A decline in the cover of grasses, an increase in cover of bryophytes and forbs and the development of a more diverse sward (a reversal of the impacts of increased SO_x) was related to decreased SO_x deposition. However there was no evidence of a recovery from SO_x deposition in the Acid or *Lolium* grasslands. Despite a decline in NO_x deposition between the two surveys we found no evidence of a reversal of the impacts of increased N deposition. The climate also changed significantly between the two surveys, becoming warmer and wetter. This change in climate was related to significant changes in both the cover and species richness of bryophytes, Cyperaceae, forbs, Poaceae and Juncaceae but the changes differed between habitats.

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1. Introduction

Grasslands are among the most extensive ecosystems in the world. Depending on the definition used, grasslands cover between 20 and 40% of the terrestrial area of the earth (Food and Agriculture Organization of the United Nations, 2005). Grasslands provide high levels of ecosystem services and are commonly managed to maximise their supply, particularly production services, for human benefit. Although many grasslands were created, and are currently being maintained, by human activities human-induced environmental perturbations are acknowledged threats to their biodiversity and functioning, with atmospheric pollution, climate change and land management being three of the most influential drivers (Millennium Ecosystem Assessment, 2005; UK National Ecosystem Assessment, 2011). These drivers operate over local to global scales and from short to decadal time-periods, with progressive change reflecting, amongst other factors, changing policies, regulation and

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global weather patterns. Therefore, while experiments can assess short-term impacts of these drivers, long-term and large-scale repeated surveys are required to fully assess the impact of spatial and temporal changes in these drivers.

Atmospheric pollution, particularly nitrogen (N) deposition, is well known as a major driver of change in many habitats around the world (Barron et al., 2014; Bobbink et al., 2010; Phoenix et al., 2006) and was identified as a major threat in the conservation of grasslands by European policy-makers (Stevens et al., 2011b). Most studies have focused on acid grasslands where N deposition has been shown to decrease species richness and diversity, increase the cover of grasses and other competitive species and decrease the cover of diminutive species such as some forbs (Damgaard et al., 2011; Dupre et al., 2010; Field et al., 2014; Stevens et al., 2011a, 2016). Increased N deposition has also been shown to increase the abundance of N-demanding plants; as shown by an increase in plants with high Ellenberg N scores (Maskell et al., 2010; Smart et al., 2003).

N deposition occurs in two forms, NO_x and NH_y. In the UK, NO_x emissions have decreased from a peak of around 900 Gg-N yr^{-1} in 1990 to about 350 Gg-N yr^{-1} in 2010 resulting in a significant decline in NO_2 concentration over the UK of about 50% and a 24% decline in wet deposition (RoTAP, 2012). Emissions of NH_y in the UK peaked in the 1980s and have decreased by about 15% since then, with around 250 Gg-N being emitted in 2010 (RoTAP, 2012). Despite the declines in emissions, however, NH_y deposition in the UK has changed little over the last 20 years due to continued transboundary movement of NH_y from overseas (RoTAP, 2012). Overall there have been small increases in NH_y in remote regions of the UK and small declines in regions in which pig and poultry emissions dominate the sources (RoTAP, 2012). Although there are differences in responses between species and habitats different forms of nitrogen deposition (NO_x or NH_y) have been shown to impact plant communities in different ways. Nitrogen deposition can directly affect the plant community via the phytotoxic effects of NO_x and NH_y and indirectly affect the plant community via eutrophication, soil acidification and increased availability of toxic metals in the soil caused by NH_y (Bobbink et al., 2010; Bobbink and Hicks, 2014; Dorland et al., 2013; Pannek et al., 2015). NO_x is associated with higher energy costs for the plants, as it is not so readily taken up as NH_y, but NO_x can counteract the acidification effects of NH_y (Dorland et al., 2013; Pannek et al., 2015).

Like N deposition, sulphur (S) deposition can impact plant communities both directly through phytotoxic effects and indirectly via increased soil acidity and increased availability of toxic metals resulting in a decline in grassland species richness and an increase in the grass:forb ratio (Damgaard et al., 2013; Henrys et al., 2011; McGovern et al., 2011). Sulphur emissions in the UK have significantly decreased, from a peak of around 3200 Gg-S in 1970, to 203 Gg-S in 2010; this has resulted in a significant decline in S deposition across the UK. Wet deposition of anthropogenic S in 2008 was 85 Gg-S compared to 252 Gg-S in 1986, a reduction of approximately 70% (RoTAP, 2012). Dry deposition of S has declined from 390 GgS yr^{-1} in 1986 to 32 Gg-S yr^{-1} in 2008 (RoTAP, 2012). Following the decrease in S emission, soils in the UK started to recover from acidification, with long-term monitoring showing soil pH increasing across a range of habitats (Morecroft et al., 2009). For many years there appeared to be a lag effect in recovery of the vegetation (McGovern et al., 2011; Morecroft et al., 2009) with the vegetation not responding significantly to the decrease in soil acidity. However, more recent work (Rose et al., 2016) across the same network of sites as Morecroft et al. (2009) reported significant increases in species richness and increases in species characteristic of less acid soils, which the authors concluded were likely to be driven by the large reductions in acid deposition in recent decades.

Atmospheric pollution is not the only driver affecting grasslands across Europe, with agricultural management (both intensification and abandonment) and climate change being listed in the top five drivers by European policy-makers (Stevens et al., 2011b). The impact of climate change on grasslands depends on which climatic factors alter and where the grasslands are located. In perennial grassland in the French Massif Central, taxonomic diversity showed no response to climate treatments (warming, summer drought and elevated CO_2) but the relative abundance of grasses decreased under both warming and simultaneous application of warming, summer drought and elevated CO_2, and legume relative abundance increased in all warmed treatments (Cantarel et al., 2013). In calcareous grasslands in Southern England, simulated climate change of warmer winters with increased summer rainfall resulted in plant cover and species richness significantly increasing (Sternberg et al., 1999). In contrast, experiments with the same levels of simulated climate change on calcareous grasslands in Northern England concluded that compositional changes were less than short-term fluctuations in species abundances driven by inter-annual climate fluctuations (Grime et al., 2008). Pakeman et al. (2015) also found very limited evidence of climate change driven species change for coastal grasslands in Scotland.

Grasslands are nearly always maintained in a pre-climax vegetation state by grazing, but the intensity, timing, duration and type of grazing animals present have all been shown to influence the plant community composition and the sward structure (Ball, 1974; Bullock et al., 1994; Grant et al., 1996; Marriott et al., 2009; Moore et al., 2015; Smith and Rushton, 1994; Stewart and Pullin, 2006). Heavy grazing can result in the dominance of grazing-tolerant species such as *Nardus stricta* and *Molinia caerulea* while light grazing can result in smaller forbs being shaded out by competitive grass species and ultimately, if seed sources are available, the establishment of woody species. In the EU, the Common Agricultural Policy (CAP), particularly in relation to agri-environment schemes, has heavily influenced the intensity and timing of grazing by domestic livestock in grassland systems (Corbelle-Rico et al., 2015; Dobrev et al., 2014; Mouysset, 2014; Pe'er et al., 2014; Schulz, 2015; Trubins, 2013). In the 1990's there was an increase in livestock numbers but, following the decoupling of livestock numbers from payment within CAP, livestock numbers have declined with destocking and abandonment occurring in many areas within Europe (Acs et al., 2010; SAC, 2008).

The impacts of changes in climate, pollution and grazing on grasslands will interact and their effects may take decades to be seen. Only long-term repeat survey work over a large area can enable us to explore and identify how grasslands respond to these different drivers and the relative importance of these drivers. Using a survey of grassland vegetation plots across Scotland, first carried out between 1958 and 1987 and resurveyed between 2012 and 2014, we test: 1) whether changes in species richness and cover of bryophytes, Cyperaceae, forbs, Poaceae, and Juncaceae over 26–55 years can be explained by changes in: a) S, NO_x and NH_y deposition; b) climate; and/or: c) grazing intensity; 2) whether different grassland habitats respond differently to changes in pollution deposition, climate and grazing; and: 3) whether the relative importance of pollution, climate and grazing in explaining variation in grassland species composition has changed between the two surveys.

2. Method

2.1. Vegetation surveys

Between 1958 and 1987 Birse and Robertson compiled 1980 records of vegetation composition in grasslands across Scotland

(Birse, 1980, 1984; Birse and Robertson, 1976). Homogeneous stands of vegetation, representative of the plant community being described, were selected for sampling, and species covers (including all bryophytes and macro-lichens) were recorded on the Domin scale (Birse and Robertson, 1976; Table S1). Plot sizes were generally 4 m^2, although occasionally plots of 1 m^2, 2 m^2 and 10 m^2 were used. Information on locality, geographical co-ordinates (British National Grid to the nearest 100 m), altitude, slope, aspect, general vegetation cover and topographic position were also recorded.

Between 2012 and 2014, 561 (28%) of these plots from across Scotland (Fig. 1) were resurveyed at a same time of year as the original survey and following a methodology as close as possible to that of the original surveyors. The majority of these plots (78%) were originally surveyed between 1967 and 1977, 10% was surveyed between 1958 and 1966 and 12% between 1978 and 1987. Since no permanent markers were in place, plots were re-located from the original geographic co-ordinates with the exact location of the sampling plot being based on the description of topographic position, slope and aspect in the original record and, where there was variability in vegetation composition, was selected to be as similar as possible to the community described in the original record. This ensured that all measures of vegetation change were conservative (Ross et al., 2010). Any plot which could not be confidently re-located was discarded. At each location, vegetation composition was recorded in the same size sampling plot as used in the original survey to ensure comparisons were valid. Cover of all species was recorded as percentages for values > 1% and as Domin categories for species with cover <1%. Both the original survey and this resurvey were part of a wider survey of vegetation in habitats across Scotland, see Britton et al. (2009, 2017) for further details of both the original survey and the resurvey methodology.

2.2. Environmental data

Pollution data (NO_x, NH_y and SO_x) was included in the analyses as cumulative deposition for the 10 years prior to the survey. Pollution data surfaces for NO_x, NH_y and SO_x each year from 1948 to 2014 were created by combining predictions from the CBED-model for 2005 (Smith et al., 2000) and published historical scaling factors (a sequence of numbers referenced to 2004 deposition data used to produce historical deposition levels (Fowler et al., 2005). Cumulative deposition for each of the three pollutants was calculated for the ten years prior to each sampling survey for each of the 561 plots. Thus the 10 year cumulative deposition was from the date of the actual visit for each individual plot. Using cumulative data over the 10 years prior to each survey allowed us to average out variability in deposition but to also assess the impact of declines in deposition which would not have been possible if cumulative deposition over a longer time period encompassing both survey periods had been used.

Climate data (rainfall, maximum temperature and minimum temperature) were included in the analyses as the yearly average for the 10 years prior to the survey. Climate data were assembled

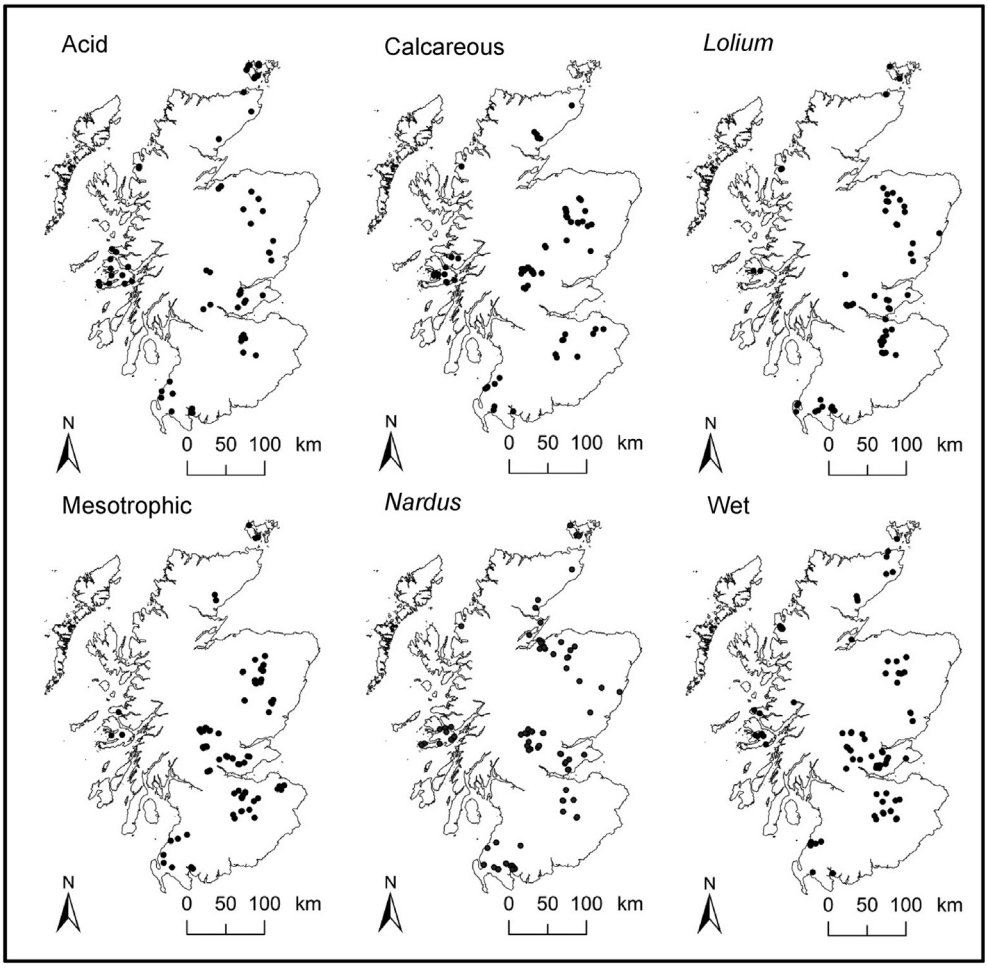

Fig. 1. Location of grassland plots by habitat.

from the UKCP09 5 km × 5 km gridded data (Perry and Hollis, 2005) for 1941 to 2011. These data have been interpolated to generate a gridded dataset from irregularly spaced station data using information on latitude, longitude, altitude, terrain shape, coastal influence and urban land use. To reduce the number of potential (and highly correlated) explanatory variables available for analysis, only monthly precipitation data summed to give yearly values and the months with the most extreme mean monthly maximum and mean monthly minimum temperature values were used. For each of these three variables, means were calculated for the ten years prior to each survey for each sample. Ten years was considered enough time to allow for differences to occur between sampling periods and to reduce the influence of exceptional years. As the gridded climate data were limited to grid cells with significant land present, climate data for a small number of coastal samples were manually averaged from the available adjacent cells.

Livestock Units were included in the analysis as the mean of the previous ten years prior to the survey. Densities of cattle and sheep were obtained for each 2 km × 2 km grid square for Scotland from the June Agricultural Census data (http://edina.ac.uk/agcensus/). Data were not available for every year from the start of this dataset in 1969. Gaps post-1969 were filled by linear interpolation between available years; for example 1980 figures were calculated as the mean on 1979 and 1981 data. Data for years prior to 1969 were estimated using the 1969 grid data multiplied by the ratio of livestock numbers in the agricultural region in the year of interest and in 1969. This assumed a constant pattern of animal distribution in the region, but was the only realistic method of estimating animal densities prior to 1969. Regional livestock numbers were taken from published reports of the Department of Agriculture for Scotland (1952 through to 1970). Densities of cattle and sheep were combined by converting to Livestock Units (LU ha^{-1} yr^{-1}, European Commission 2009). The mean of the previous ten years of Livestock Units was then calculated for each sample to smooth out short-term variations in grazing intensity.

2.3. Data cleaning

The data were checked for consistency of species nomenclature between surveys, and any species not thought to have been recorded with equal rigour in both surveys were removed. Species which are difficult to separate consistently or have been affected by taxonomic changes were amalgamated at the genus level. The resulting dataset comprised 484 species (or species amalgams) recorded across 561 plots. The re-survey cover data were converted to Domin categories, before both original and re-survey data were back-transformed to percentage cover, using the mid-point of each Domin category (Table S1), to ensure standardisation of the two datasets. The percentage cover was then converted to a proportion of the total cover, to ensure standardisation between the two surveys (preliminary analysis suggested that total cover estimates in the resurvey were higher than the original survey).

Plots were assigned to the UK's National Vegetation Classification (NVC) (Rodwell, 1992) based on analysis of the original survey data by the programme Tablefit (Hill, 1996). The 32 NVC classes were then amalgamated into six different grassland habitats: Acid, Calcareous, *Lolium* (dominated by *L. perenne*), Mesotrophic, *Nardus* (dominated by *N. stricta*) and Wet (Table 1). Details of changes in the species present within these six habitats is provided by (Mitchell et al., 2017). Analysis was carried out separately for each habitat as it was considered likely that the impact of the environmental variables on vegetation composition would differ between habitats differing in productivity and dominant species.

Species were classified into the following groups: bryophytes, Cyperaceae (all sedges), forbs, Poaceae, Juncaceae, dwarf shrubs, trees/shrubs, lichens and Pteridophyta (ferns). There were insufficient plots with data for the last four groups so these were removed from the analysis of species group responses. Total cover and species richness was calculated for each of the remaining five species groups for each plot and survey.

2.4. Data analysis

Changes in the drivers between the two surveys were assessed using mixed models (PROC MIXED in SAS (SAS, 2015)) with the difference between the values corresponding to the two surveys as the response variable and the intercept as the only fixed effect. An exponential spatial correlation structure was used to model the spatial autocorrelation in the residuals and tests were performed using the residual degrees of freedom.

The relationship between change in cover of each plant species group against the change in the environmental variables was assessed using General Linear Models (the PROC GLM function in SAS (SAS, 2015)). As species richness is count data it was not possible to analyse the change because this would result in negative integers. Instead we analysed the counts from the two surveys using Generalized Linear Models with a Poisson error term and a log link function (PROC GLIMMIX in SAS (SAS, 2015)). Survey was included in the model in addition to the environmental drivers; plot number was included as a fixed effect in order to account for differences between plots and allow differences within plots (i.e. change) to be investigated. In both models the significance of each variable was assessed once the variation explained by the other drivers had been accounted for.

Variation partitioning using Redundancy Analysis (RDA) in CANOCO v5 (ter Braak et al., 2012) was carried out on the species composition data for each survey. The variation in the species composition was partitioned into three: that due to pollution (NO_x, NH_y, SO_x), climate (rain, maximum temperature, minimum temperature) and grazing (livestock units). Within each group of variables forward selection was used to select those environmental drivers that explained a significant amount of the variation ($P < 0.05$). In all forward selection analyses the adjusted P value (adjusted to take account of false discovery rate) was used. Significance was assessed using a Monte-Carlo permutation test (9999 permutations) in which residuals from the reduced model were permuted.

3. Results

3.1. Change in drivers

There was a significant difference between surveys in ten year cumulative S deposition ($P < 0.001$), with significant declines ($P < 0.0001$) in all habitats (Table 2). These declines ranged between 31 and 286 kg SO_x ha^{-1}. Ten year cumulative NO_x deposition also declined between the two surveys ($P < 0.0001$), with significant declines ($P < 0.001$) in all habitats. Declines ranged from 4 to 50 kg NO_x ha^{-1}. Cumulative ten year NH_y deposition significantly ($P < 0.05$) increased in all habitats except Calcareous and *Nardus* grasslands (Table 2). Annual average rainfall significantly increased ($P < 0.001$) between the two surveys in all habitats (Table 2), with an average increase of 244 mm (c. 15%). Average monthly maximum temperature over the ten years previous to the survey increased by on average 1.2 °C with a significant difference between surveys ($P < 0.0001$) in all habitats. Average monthly minimum temperature was also significantly different between surveys ($P < 0.0001$) with an average increase of 0.7 °C and significant ($P < 0.05$) increases in all grassland habitats. Changes in ten year average livestock units ranged from −75 LU to 90 LU with no overall significant

Table 1
Habitat types used in the analysis together with the National Vegetation Classification communities (Rodwell, 1992) used in their construction.

Habitat	Plots *n*	EUNIS code	Annex I Code	NVC class	NVC *n*
Acid (Acid grassland)	96	E1.92	None	U1	4
		E1.72#/(E1.72x)	H6230/(None)	U4acde	84
		E4.116	None	U13	1
		E5.31/(B3.31)	None/(H1230)	U20	5
		G1.83	H91A0	W11	1
		B1.41	H2130	SD12	1
Calcareous (Calcareous grassland)	86	E1.26	H6210	CG2	1
		E1.72/(B3.31) (B1.41)	H6230/(H1230) (H2130)	CG10	69
		E1.72	H6230	CG11	16
Lolium (Improved grassland)	78	E2.11/(E2.12)	None	MG6	37
		E2.6	None	MG7	41
Mesotrophic (Mesotrophic and semi-improved grassland)	92	E1.72	None	U4b	57
		B1.41/(B1.9)	H2130/(H21A0)	SD8	3
		E2.21	None	MG1	1
		E2.24	H6520	MG3	1
		E2.11	None	MG5	22
		E3.41	None	MG8	6
		B2.4	H1220	MC9	2
Nardus (Mat grass and Heath rush pasture)	113	E3.52/E1.72/(E1.71)	None/H6230/(None)	U5	93
		E3.52	None	U6	17
		F4.11	H4010	M15	3
Wet (Wet pasture)	97	D2.22	None	M6	16
		D4.15	H7230	M10	9
		E3.41	None	M22	2
		E3.42/(E3.41)	None	M23	40
		E3.51	H6410	M24	13
		E3.512	None	M25	2
		E3.511	H6410	M26	7
		E5.42	None	M27	4
		E3.41	None	MG9	2
		E3.44	None	MG10	1
		B1.84	H2190	SD17	1

Table 2
Mean drivers (± 1SE). SO_x, NH_y and NO_x are cumulative data for the 10 years prior to the survey (kg ha^{-1}). Rain (mm) is the mean annual rainfall for the 10 years prior to the survey. MaxT and MinT are the mean monthly maximum and minimum temperatures (°C) for the 10 years prior to the survey. LU is the mean Livestock units for the 10 years prior to the survey. Significant differences between surveys are indicated by * = P < 0.05, ** = P < 0.01, *** = P < 0.001 after the repeat survey together with the direction of change ↑ = increase, ↓ = decrease. ns = not significant.

Habitat	Survey	SO_x		NH_y		NO_x		Rain		MaxT		MinT		LU	
Acid	1	169 ± 6.3		55 ± 2.5		72 ± 2.8		1176 ± 38		17 ± 0.1		−1.6 ± 0.1		48 ± 3.3	
	2	49 ± 1.8	↓***	58 ± 2.7	↑*	52 ± 2.0	↓***	1396 ± 50	↑***	18 ± 0.1	↑***	−0.8 ± 0.1	↑**	43 ± 3.8	ns
Calcareous	1	186 ± 7.9		60 ± 2.5		85 ± 3.5		1314 ± 43		16 ± 0.2		−2.0 ± 0.1		34 ± 2.8	
	2	53 ± 2.1	↓***	63 ± 2.6	ns	60 ± 2.4	↓***	1671 ± 71	↑***	17 ± 0.2	↑***	−1.5 ± 0.2	↑***	33 ± 3.8	ns
Lolium	1	146 ± 5.7		53 ± 2.3		66 ± 2.5		1072 ± 29		17 ± 0.2		−1.1 ± 0.2		59 ± 4.0	
	2	44 ± 1.8	↓***	55 ± 2.5	↑*	48 ± 1.8	↓***	1228 ± 38	↑***	18 ± 0.2	↑***	−0.3 ± 0.2	↑***	70 ± 5.6	↑***
Mesotrophic	1	134 ± 4.7		47 ± 2.0		59 ± 2.1		1142 ± 30		16 ± 0.2		−0.5 ± 0.2		42 ± 3.3	
	2	40 ± 1.4	↓***	49 ± 2.2	↑*	42 ± 1.5	↓**	1348 ± 49	↑***	17 ± 0.1	↑***	0.2 ± 0.2	↑**	43 ± 3.7	ns
Nardus	1	194 ± 6.8		68 ± 2.1		88 ± 2.7		1222 ± 32		16 ± 0.1		−2.2 ± 0.1		42 ± 2.1	
	2	57 ± 1.9	↓***	71 ± 2.3	ns	64 ± 1.8	↓***	1485 ± 45	↑**	18 ± 0.1	↑***	−1.6 ± 0.1	↑*	34 ± 2.3	ns
Wet	1	165 ± 8.3		60 ± 2.8		73 ± 3.3		1169 ± 41		17 ± 0.1		−1.3 ± 0.1		48 ± 2.9	
	2	50 ± 2.5	↓***	64 ± 3.0	↑***	53 ± 2.4	↓***	1403 ± 54	↑***	18 ± 0.1	↑***	−0.6 ± 0.1	↑***	50 ± 4.0	ns

change between surveys. However there was a significant increase in *Lolium* grasslands (Table 2). There were correlations between the changes in drivers (Table S2). In particular a positive correlation between change in SO_x and change in NO_x.

The differences between habitats in changes in the drivers may be due to differences in their mean geographical location. While all habitats were spread across Scotland (Fig. 1), there were significant differences in mean Northing ($F_{5,555} = 7.10$; $P < 0.0001$) and Easting ($F_{5,555} = 3.38$; $P < 0.0001$). Mean Northing increased in the order *Nardus*, Wet, Acid, Calcareous, *Lolium*, Mesotrophic and mean Easting increased in the order Wet, Calcareous, Acid, Mesotrophic, *Lolium*, *Nardus*. In addition, there were significant differences in mean altitude between habitat types ($F_{5,555} = 49.4$; $P < 0.0001$) with the mean altitude increasing in the order Mesotropic, *Lolium*, Wet, Acid, Calcareous, *Nardus*.

3.2. Changes in cover of species groups in relation to changes in drivers

A decline in ten year cumulative SO_x deposition was related to an increase in cover of bryophytes in Mesotrophic and *Nardus* grasslands and forbs in Wet grasslands (Table 3). In contrast Poaceae cover declined as S deposition decline in Calcareous and *Nardus* grasslands. A decline in ten year cumulative NO_x deposition was related to a decrease in the cover of bryophytes in Mesotrophic and *Nardus* grasslands and forbs in Wet grasslands. In contrast Poaceae cover increased as NO_x deposition decreased in *Nardus* grasslands. An increase in ten year cumulative NH_y was related to a decrease in forb cover in Wet grasslands.

An increase in average annual rainfall was related to an increase in bryophyte cover in Acid grasslands (Table 3). An increase in

Table 3
Results of General Linear Models of change in cover of species groups against change in pollution, climate and grazing in six grassland habitats. NO_x, NH_y and SO_x = change in cumulative pollution deposition for the ten years prior to each survey. Rain = change in 10 year average rainfall. Tmax and Tmin = change in 10 year average of the mean monthly maximum (MaxT) and minimum (MinT). LU = change in 10 year average livestock units. ↓ = negative relationship, ↑positive relationship. P values for individual drivers are shown: *P < 0.05, **P < 0.01, ***P < 0.001. Adjusted R^2 values for the whole model are shown with all environmental drivers included. ns = none of the drivers were significant. Effect sizes, estimates of the mean and standard errors are shown in Tables S3-S7.

	Acid	Calcareous	*Lolium*	Mesotrophic	*Nardus*	Wet
Bryophyte	Rain↑* LU↓* $R^2 = 0.06$	ns	ns	SO_x↓** NO_x↑** $R^2 = 0.06$	SO_x↓** NO_x↑ ** $R^2 = 0.19$	MaxT↓* $R^2 = 0.08$
Cyperaceae	LU↑* MaxT↓* $R^2 = 0.18$	ns	ns	ns	ns	ns
Forbs	LU↑** $R^2 = 0.09$	MinT↑* $R^2 = 0.10$	ns	ns	ns	SO_x↓** NH_y↓* NO_x↑** $R^2 = 0.07$
Poaceae	ns	SO_x↑ * LU↑** $R^2 = 0.18$	ns	ns	SO_x↑** NO_x↓** $R^2 = 0.16$	LU↑* $R^2 = 0.04$
Juncaceae	ns	MinT↑ * $R^2 = 0.10$	ns	LU↑** $R^2 = 0.03$	MinT↑* $R^2 = 0.05$	ns

maximum temperature was related to a decrease in the cover of bryophytes in Wet grasslands and Cyperaceae in Acid grasslands. An increase in minimum temperature was related to an increase in forb cover in Calcareous grasslands and Juncaceae cover in Calcareous and *Nardus* grasslands.

The decline in ten year average livestock units in acid grasslands was related to an increase in bryophyte cover and a decline in Cyperaceae and forb cover. There was a positive relationship between livestock units and Poaceae cover in both Calcareous and Wet grasslands: livestock units and Poaceae cover declined in Calcareous grasslands and livestock units and Poaceae cover increased in Wet grasslands. The increase in livestock units in Mestotrophic grasslands was related to an increase in Juncaceae cover.

3.3. Changes in species richness of species groups in relation to changes in drivers

Declines in ten year cumulative S deposition were related to increasing total species richness in *Nardus* grasslands and increasing species richness of bryophytes (*Nardus* grasslands), Cyperaceae (Calcareous and *Nardus* grasslands) and Juncaceae (*Lolium* and Mesotrophic grasslands) (Table 4). In contrast declines in S deposition were related to declines in Cyperaceae species richness in *Lolium* grasslands. Decreases in ten year cumulative NO_x deposition were related to declines in total species richness in *Lolium* grasslands and declines in species richness of bryophytes (*Nardus* grasslands), Cyperaceae (Calcareous grasslands), Poaceae (*Lolium* and Wet grasslands) and Juncaceae (*Lolium* and Mesotrophic grasslands). Increases in ten year cumulative NH_y deposition were related to decreases in total species richness in Calcareous, Mesotrophic and *Nardus* grasslands. In addition increases in NH_y deposition were related to decreases in species richness of bryophytes (Calcareous, Mesotrophic and *Nardus* grasslands), Cyperaceae (Calcareous and Mesotrophic grasslands), forb (Mesotrophic grasslands) and Juncaceae (Mesotrophic grasslands). In contrast increased forb and Juncaceae species richness was related to increased NH_y deposition in Acid and *Lolium* grasslands respectively.

Increased average rainfall was related to increased total species richness and forb species richness in *Lolium* grasslands. Increased average minimum temperature was related to increased total species richness in *Nardus* grasslands and increased species richness of forbs (Calcareous grasslands) and Juncaceae (*Nardus* grasslands). In contrast in other habitats some species groups had a negative relationship with increased minimum temperature. Species richness of bryophytes (Wet grasslands), forbs (acid grasslands) and Juncaceae (*Lolium* grasslands) declined with increasing minimum temperatures. Increased maximum temperatures were related to a decrease in Cyperaceae species richness (Mesotrophic grasslands) and an increase in Poacease species richness (Wet grasslands).

The decline in livestock units in Acid and *Nardus* grasslands was related to a decline in forb species richness (Acid grasslands) and total species richness and bryophyte richness (*Nardus* grasslands). The increase in livestock units in *Lolium* grasslands was related to a decrease in Cyperaceae and Juncacease species richness.

3.4. Variation partitioning

The three groups of drivers, pollution, climate and grazing, explained between 5% (Mesotrophic and Wet grasslands) and 14% (Calcareous grasslands) of the variation in species composition in the first survey and between 3% (Mesotrophic grasslands) and 14% (*Nardus* grasslands) in the second survey (Table 5). The relative importance of these three groups of drivers in explaining variation in grassland species composition changed very little between the two surveys (Table 5). In the grasslands regarded as less intensively managed (Acid, Calcareous and *Nardus*), pollution and climate explained more of the variation in species composition than grazing for both surveys. In *Lolium* grasslands. grazing explained a similar amount of variation as pollution in the first survey but less than climate, whereas in the re-survey grazing explained less variation than both pollution and climate. In Mesotrophic grasslands, pollution did not explain any of the variation in either survey, grazing explained less variation than climate in the first survey, but a similar amount to climate in the re-survey. However these changes between the two surveys in the relative importance of pollution, grazing and climate in *Lolium* and Mesotrophic grasslands were only due to changes in the amount of variation explained by each of these groups of drivers of 3% or less. In Wet grassland, climate explained the most variation in both surveys while grazing did not explain any of the variation in species composition in either survey.

Table 4
Results of Generalized Linear Mixed Models of change in species richness of species groups against change in pollution, climate and grazing in six grassland habitats. NOx, NHy and SOx = change in cumulative pollution deposition for the ten years prior to each survey. Rain = change in 10 year average rainfall. Tmax and Tmin = change in 10 year average of the mean monthly maximum (MaxT) and minimum (MinT). LU = change in 10 year average livestock units. ↓ = negative relationship, ↑positive relationship. P values for individual drivers are shown: *P < 0.05, **P < 0.01, ***P < 0.001. ns = none of the drivers were significant. Results from models including all environmental drivers are shown. Effect sizes, estimates of the mean and standard errors are shown in Tables S8-S13.

	Acid	Calcareous	*Lolium*	Mesotrophic	*Nardus*	Wet
All species	ns	NH_y↓*	Rain↑* NO_x↑*	NH_y↓**	SO_x↓* NH_y↓* MinT↑* LU↑*	ns
Bryophyte	ns	NH_y↓*	ns	NH_y↓*	SO_x↓*** NH_y↓*** NO_x↑* LU↑*	MinT↓*
Cyperaceae	ns	SO_x↓* NH_y↓* NO_x↑*	SO_x↑* LU↓***	NH_y↓* MaxT↓*	SO_x↓*	ns
Forbs	NH_y↑** LU↑** MinT↓*	MinT↑*	Rain↑*	NH_y↓*	ns	ns
Poaceae	ns	ns	NO_x↑*	ns	ns	NO_x↑* MaxT↑*
Juncaceae	ns	ns	SO_x↓** NH_y↑*** NO_x↑*** LU↓*** MinT↓***	SO_x↓** NH_y↓* NO_x↑*	MinT↑*	ns

Table 5
Percentage variation in vegetation species composition data uniquely explained by pollution, climate and grazing. P values are from a Monte Carlo permutation test with 9999 permutation. Variables in parentheses are significant drivers selected by manual forward selection in variation partitioning: SOx, NHy and NOx are cumulative data for the 10 years prior to the survey (kg ha-1). Rain (mm) = the mean annual rainfall for the 10 years prior to the survey. MaxT and MinT are the mean monthly maximum and minimum temperatures (°C) for the 10 years prior to the survey. LU is the mean Live Stock units for the 10 years prior to the survey. ns = not significant. ∩ = intersection in variation, i.e. explained by more than one group of drivers.

	Survey	Pollution (P)	Climate (C)	Grazing (G)	P∩C	C∩G	P∩G	P∩C∩G	Unexplained
Acid	1	3.5% ns (SO_x, NH_y, NO_x)	3.7% ns (Rain, MinT)	0.9% ns (LU)	1.2%	0.6%	0.6%	0.1%	89%
	2	4.1% P = 0.002 (SO_x, NH_y, NO_x)	2.6% ns (MaxT, MinT)	1.8% P = 0.003 (LU)	1%	0.3%	0.3%	0.2%	90%
Calcareous	1	4.9% P = 0.0001 (SO_x, NH_y, NO_x)	6% P = 0.0001 (Rain, MinT, MaxT)	1.2% ns (LU)	1%	0.3%	0.5%	0%	86%
	2	5.2% P = 0.011 (SO_x, NH_y, NO_x)	4% P = 0.0001 (Rain, MinT)	1% ns (LU)	0.6%	0.3%	0.5%	0.1%	88%
Lolium	1	1.7% ns (NH_y)	5.6% P = 0.0002 (MinT, MaxT)	1.5% ns (LU)	0.3%	0.9%	0.2%	0%	89.8%
	2	3.2% ns (SO_x,, NO_x)	3.3% P = 0.019 (MaxT, MinT)	2.1% P = 0.002 (LU)	1.1%	0.4%	0.5%	0%	89.4%
Mesotrophic	1		3% P = 0.0034 (MinT, MaxT)	1.3% ns (LU)		0.3%	3%		95.4%
	2		1.7% P = 0.0113 (MinT)	1.6% P = 0.0112 (LU)		0.1%			96.6%
Nardus	1	5.0% P = 0.0001 (SO_x, NH_y, NO_x)	4.6% P = 0.0001 (Rain, MinT, MaxT)	1.1% ns (LU)	1.4%	0.3	0.5%	0.2%	86.9%
	2	5.1% P = 0.0002 (SO_x, NH_y, NO_x)	5.1% P = 0.002 (Rain, MinT, MaxT)	1.2% P = 0.047 (LU)	1.4%	0%	0.3%	0.4%	86.5%
Wet	1	1.2% ns (NH_y)	4.3% P = 0.0002 (Rain, MaxT, MinT)		0.4%				94.1%
	2	2.5% ns (SO_x, NO_x)	2.8% P = 0.0017 (Rain, MinT)		0.5%				94.2%

4. Discussion

Our study provides one of the few examples of plant communities starting to recover following a decrease in SO_x deposition. Most research on the impacts of atmospheric deposition to date have studied the impact of increased pollution or the impact of cumulative deposition. If cumulative deposition is used as the sole environmental driver an assumption is thereby made that ecosystem recovery from deposition impacts is not possible (Stevens et al., 2016). The predicted slow lag time between a decrease in deposition and seeing a response has been suggested as a reason for excluding recovery from some models of impacts (Stevens et al., 2016). However, policy-makers require evidence to assess whether policy decisions to reduce emissions are having a positive environmental impact (Rowe et al., 2014) and there is a shortage of such studies (Stevens et al., 2016), but see Rose et al. (2016). Here we have shown that 40 years after the peak of SO_x emissions, decreases in SO_x are related to significant changes in species richness and/or cover in some species groups in Scottish Calcareous, Mestrophic, *Lolium*, *Nardus* and Wet grasslands.

Our results suggest that where SO_x deposition has declined there has been a decline in the cover of dominant grass species, an increase in cover of bryophytes and forbs and the development of a more diverse sward, i.e. a reversal of the impacts of increased SO_x. These changes were probably driven by an increase in soil pH due to the reduction in SO_x deposition (McGovern et al., 2011; Rose et al., 2016). Although the effect size of S on species richness or cover was low the magnitude of the decline in S resulted in noticeable changes in species composition (Mitchell et al., 2017). While S deposition has decreased dramatically between these two surveys deposition is still high compared to pre-industrial levels (RoTAP, 2012). Therefore the magnitude and rate of recovery may be limited, although, to the author's knowledge, there are no studies assessing the rate of recovery following S deposition decline.

There was no evidence of declines in NO_x deposition leading to a reversal of the impacts of N deposition on grassland plant communities. This may be because the declines in NO_x were much smaller than the declines in SO_x. Our study suggests that NO_x and NH_y are having opposite effects on cover and species richness with

a positive effect of NO_x and a negative effect of NH_y. This is consistent with other studies that have suggested that NH_y may be driving changes via acidification while NO_x is countering this by providing nutrients (Dorland et al., 2013; Pannek et al., 2015). Many previous studies have shown a decrease in species richness with increased NH_y (Stevens et al., 2004, 2010, 2011a) similar to the patterns we found in this study.

The change to a warmer and wetter climate seen over the 26–55 years between these two surveys also appeared to have a significant effect on grassland composition, contrary to the short-term (13 year) climate manipulation experiments of Grime et al. (2008). The results suggest that a wetter climate may be beneficial for species diversity in *Lolium* grasslands where species richness increased. However, the warmer climate may be detrimental to some species groups, as indicated by a decrease in species richness of forbs in Acid grasslands, bryophytes in Wet grasslands and Cyperaceae in Mesotrophic grasslands. These results concur with the experimental work of Sternberg et al. (1999) who found decreased species richness with warmer winters but increased species richness in plots with supplemented rainfall in the summer. In contrast other species groups, in other habitats benefit from increased temperatures, such as the increased forb species richness in Calcareous grasslands.

Changes in livestock units explained very few of the changes in species richness and cover. The peak in livestock units in Scotland occurred in the 1990's (Aspinall et al., 2011) between the two surveys. So comparing changes between the 10 years preceding each survey may have masked the impact of this peak. Nonetheless where species richness was related to livestock units there was a pattern of increased species richness with increased grazing in the less intensively managed habitats and decreased species richness with increased grazing in the most intensively managed habitat (*Lolium*). This illustrates that an optimum grazing intensity exists with too high or low grazing pressure resulting in a decline in species richness.

The relative importance of pollution, climate and grazing in explaining variation in the species composition of the six habitats showed little change between the surveys (RDA results). It was the analysis of the change in these drivers in relation to changes in cover and species richness over time which enabled us to show the impact of these drivers. Although the amount of variation explained by these drivers was low, but not untypical of such studies (e.g. Britton et al., 2017; Britton et al., 2009), we showed that the six different grassland habitats responded differently to the different drivers. Differences in underlying geology and soils may influence how the habitats respond to changes; Acid grasslands showed no response to a decline in SO_x compared to Calcareous, Mesotrophic, *Nardus* and Wet grasslands which did. The low buffering capacity of the organic soils beneath the acid grassland may have reduced recovery from acidification in this habitat (Evans et al., 2008). Land management (reseeding, fertilisation and/or herbicide) will have influenced the results from the more intensively managed *Lolium* and Mesotrophic grasslands and may have driven some of the changes in species richness and cover reported here, but data on these drivers was not available. None of the drivers investigated here were related to the change in cover of any of the species groups in *Lolium* grasslands and it is possible that local land management are the main drivers of community composition change in this habitat.

5. Conclusion

In all habitats, responses due to pollution, climate and grazing are complex and coupled with uncertainties over lag time effects (Evans et al., 2014). This long-term resurvey has enabled us to start to quantify the lag-times of a reduction in SO_x (c. 40 years) and NO_x (more than 30 years) and provides some hope that a reversal of some of the impacts of SO_x deposition on grasslands may be possible. The results have also indicated climate change impacts on species richness and cover occurring over the last 26–55 years due to a warmer and wetter climate, although the direction of these changes, positive or negative, differ between species groups and grassland habitats.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.envpol.2017.12.086.

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